

Tamias merriami. By Troy L. Best and Nancy J. Granai

Published 2 December 1994 by The American Society of Mammalogists

***Tamias merriami* J. A. Allen, 1889**

Merriam's Chipmunk

Tamias asiaticus merriami J. A. Allen, 1889:176. Type locality "San Bernardino Mts., Cal." (due north of San Bernardino at 4,500 feet altitude, San Bernardino Co., California—Grinnell, 1933:132).

Tamias merriami: J. A. Allen, 1890:60. First use of current name combination.

Tamias pricei J. A. Allen, 1895:333. Type locality "Portola, San Mateo Co., California."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains 25 species (Wilson and Reeder, 1993). *T. merriami* is in the subgenus *Neotamias* (Levenson et al., 1985). Three subspecies of *T. merriami* are recognized (Hall, 1981):

T. m. kernensis (Grinnell and Storer, 1916:5). Type locality "Fay Creek, 4100 feet altitude, six miles north of Weldon, Kern County, California."

T. m. merriami J. A. Allen, 1889:176, see above (*mariposae* Grinnell and Storer is a synonym).

T. m. pricei J. A. Allen, 1895:333, see above.

DIAGNOSIS. *Tamias merriami* (Fig. 1) may be sympatric or parapatric with *T. amoenus*, *T. minimus*, *T. obscurus*, *T. panamintinus*, *T. quadrimaculatus*, *T. senex*, *T. speciosus* (Callahan, 1976), *T. umbrinus*, and possibly *T. alpinus* (Larson, 1986). The large size of *T. merriami* distinguishes it from sympatric and parapatric congeners, except *T. quadrimaculatus*, *T. senex*, and *T. obscurus*. From *T. quadrimaculatus* and *T. senex*, *T. merriami* differs in its longer and bushier tail, the edging of which is duller white or slightly buffy rather than pure white, in its narrower skull (Fig. 2), more recurved incisors, and presence of a notch between the tips of the nasals (Johnson, 1943). From *T. senex*, *T. merriami* may be further distinguished by its paler ears without white patches, smaller postauricular patches (Howell, 1929), and grayish rather than brownish cheeks, and from *T. quadrimaculatus* by its much paler submalar (below eye) stripes and shorter ears (Johnson, 1943).

Although *T. merriami* and *T. obscurus* appear to be geographically sympatric in the San Bernardino and San Jacinto mountains of southern California, they are elevationally allopatric and ecologically distinct. Elsewhere, *T. merriami* occurs northwestward to the Pacific coast, northward to the Sierra Nevada and southward to Baja California, whereas *T. obscurus* occurs southward into Baja California (Blankenship and Bradley, 1985; Callahan, 1976, in litt.; Hall, 1981). Spermatozoa of *T. merriami* and *T. obscurus* are similar (Callahan, 1976), but the two species can be distinguished by the ossa genitalia (Fig. 3; Blankenship, 1985; Callahan, 1977). The summer pelage of adult *T. merriami* is darker, more yellowish, and there is less reddish in the dark dorsal stripes than in *T. obscurus* (Callahan, 1977). Further, *T. merriami* is larger, has a longer tail and hind foot, and has a larger and flatter cranium. Differences are less pronounced in the San Bernardino Mountains than in other zones of sympatry, but the two species are 100% separable by discriminant analysis of skull and body measurements (Callahan, 1976, 1977). In the San Jacinto Mountains, adults of *T. merriami* and *T. obscurus* are distinguishable by ventral coloration; hairs of the throat and upper chest are whitish in *T. m. merriami* and gray (usually black at the base) in *T. o. davisii* (this criterion is not valid in the San Bernardino Mountains where these hairs have black bases in both species—Callahan, 1977).

Sonograms of the chips of *T. merriami* and *T. obscurus* are characterized by a symmetrical inverted-V shape. The calls of *T. merriami* and *T. obscurus* differ in frequency of origin of upsweep,

top of upsweep, bottom of downsweep, and length of chip (Blankenship and Brand, 1987). In addition, *T. merriami* usually is found in more mesic forest, primarily coniferous forest; *T. obscurus* is closely associated with single-leaf pinyon (*Pinus monophylla*) woodland in the San Bernardino Mountains. Habitats occupied by these chipmunks are more useful than calls in distinguishing between these species (Blankenship, 1985).

Tamias merriami cannot be distinguished from *T. obscurus davisii* on the basis of gross chromosomal morphology because both have karyotype B of *Tamias*, unlike *T. o. obscurus* and *T. o. meridionalis*, which have karyotype A of *Tamias*. Two adult specimens of *T. merriami* resemble *T. obscurus* in coloration, but the baubella and skulls are typical of *T. merriami* (Callahan, 1977). Examination of 11 allozymes indicated that *T. merriami* does not differ from *T. obscurus* in this respect (Blankenship, 1985; Blankenship and Bradley, 1985).

The baculum of *T. merriami* differs from those of *T. bulleri*, *T. cinereicollis*, *T. palmeri*, *T. panamintinus*, *T. quadrimaculatus*, *T. quadrivittatus*, *T. ruficaudus*, *T. speciosus*, and *T. umbrinus*, in that the base is incised dorsally, the shaft is thinner, and the tip is proportionately shorter. Bacula of *T. amoenus* and *T. minimus* have shorter shafts than does that of *T. merriami* (White, 1953). *T. amoenus* and *T. minimus* are smaller and more distinctly striped than *T. merriami* (Callahan, 1976).

GENERAL CHARACTERS. The tail of Merriam's chipmunk is long and bushy (75–97% of length of head and body), and the feet and ears are long and slender. The ears are sparsely furred on the convex surfaces in summer pelage, and are grayish (ochraceous near the coast). The dorsal stripes are about equal in width; the dark stripes are gray or brown, seldom with black areas, and the pale stripes are grayish. The cheeks and underparts are white and more or less dulled by gray, but in coastal areas the cheeks and underparts usually are suffused with ochraceous. The tail edging usually is dull white, but it is slightly buffy in some animals. The dorsal stripes are indistinct in the winter pelage of *T. m. kernensis*, which in this respect resembles *T. dorsalis* and *T. obscurus* (Hall, 1981).

Color variation in *Tamias merriami* appears to follow Gloger's Rule. Thus, darker populations (*T. m. pricei*) occupy redwood (*Sequoia sempervirens*) forests in humid coastal areas from San Fran-



FIG. 1. A male *Tamias merriami* near Felton, Santa Cruz Co., California. Photograph by T. L. Best.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias merriami* from near Wrightwood, Angeles National Forest, Los Angeles Co., California (female, Museum of Southwestern Biology 47378). Greatest length of cranium is 39.0 mm. Photographs by T. H. Henry.

cisco Bay southward, whereas the palest form (*T. m. kernensis*) is restricted to single-leaf pinyon forests in Walker Pass in the semiarid Kern Basin and on the eastern slope of the Sierra Nevada. None of the subspecies is geographically isolated (Callahan, 1976). This trend in coloration is paralleled by a trend in body size: *T. m. pricei* is larger than *T. m. kernensis* and *T. m. merriami*, and has a longer tail (Johnson, 1943).

Average measurements (in mm) of adult males and females of *T. m. kernensis*, *T. m. merriami*, and *T. m. pricei*, respectively, are: greatest length of cranium, 37.4, 37.8, 38.0, 38.2, 38.1, 38.7; rostral length, 13.8, 13.9, 14.0, 14.1, 13.9, 14.2; length of braincase, 23.7, 23.8, 24.1, 24.2, 24.2, 24.6; length of maxillary toothrow, 5.8, 5.9, 5.9, 5.9, 5.8, 5.9; length of nasals, 12.0, 12.3, 12.1, 12.6, 12.3, 12.8; zygomatic breadth, 20.0, 20.3, 20.4, 20.3, 20.3, 20.4; depth of cranium, 14.9, 14.9, 14.7, 14.7, 15.2, 15.1; least interorbital breadth, 8.6, 8.7, 8.7, 8.6, 8.7, 8.7; cranial breadth, 17.5, 17.5, 17.6, 17.7, 17.9, 17.9; rostral breadth, 8.7, 8.7, 8.4, 8.5, 8.7, 8.8; width of nasals, 2.6, 2.6, 2.6, 2.4, 2.4, 2.3; length of head and body, 131.4, 132.5, 133.4, 135.7, 135.4, 138.3; length of tail, 108.7, 110.3, 109.4, 109.5, 115.8, 116.3; length of hind foot, 35.5, 35.3, 35.2, 36.4, 36.6, 36.9 (Callahan, 1977). Average mass is 71.8 and 77.8 g for adult males and females, respectively (Larson, 1981; range, 53.0–88.0 g—Howell, 1929).

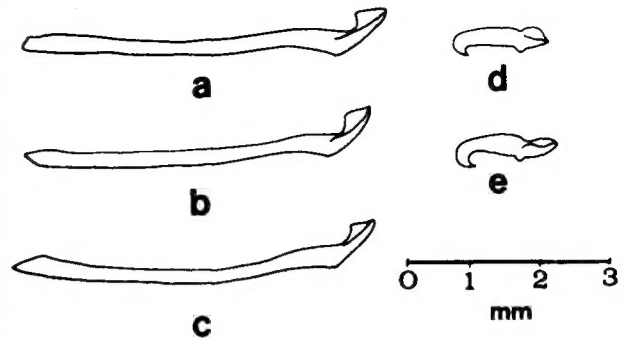


FIG. 3. Ossa genitalia of *Tamias merriami* (right, lateral view): a–c bacula; d–e baubella; a, *T. m. merriami*; b, *T. m. pricei*; c, *T. m. kernensis*; d, *T. m. merriami*; e, *T. m. pricei* (Callahan, 1977).

Mass shows fluctuation, not only within a day, but also on consecutive days (Larson, 1981).

There is no sexual dimorphism in average length of head and body (Levenson, 1990), but females of *T. m. merriami* are larger than males in length of nasals and length of hind foot. In addition, females are larger than males in length of nasals in *T. m. pricei* and in length of maxillary toothrow in *T. m. kernensis* (Callahan, 1977).

DISTRIBUTION. Merriam's chipmunk occurs on the lower western slopes of the southern Sierra Nevada, coastal ranges, and in wooded areas southward to northern Baja California (Fig. 4; Jameson and Peeters, 1988). It inhabits upper Sonoran and transition life zones at elevations from sea level (Howell, 1929) to 2,940 m (Larson, 1981).

FOSSIL RECORD. The genus *Tamias* evolved by the early Miocene (Black, 1972). No fossils of *T. merriami* are known.

FORM AND FUNCTION. Molt in all ages, beginning with postjuvenile molt, begins on the venter. On the dorsum, shedding first appears on the rhinarium and terminates on the hind feet. The tail molts annually and in regrowth is banded; the distal end of each hair is black-tipped for a short time. Quiescence and mid-summer pregnancies contribute to arrest of molt; this leaves a condition of broken overhair, the loss of which leaves the blue-black underfur exposed on the rump. Adults may have bare rumps, hairless tails, hairless bodies, or evidence of three distinct pelages (Larson, 1981).

An adult female *T. m. kernensis* in worn winter pelage on 2 July had irregular patches of summer pelage on the head and back. Molt was shown on another adult female on 10 October; winter pelage covered the rump, flanks, and posterior back. An adult male *T. m. merriami* in spring molt on 17 May had the anterior portion of the back covered with fresh summer pelage and an irregular patch of new hair on each flank. On 24 June, a female had patches of new pelage on the nape and middle of the back. Autumn molt was shown by an adult female on 28 September; winter pelage was appearing on the rump and posterior back. In *T. m. pricei*, autumn molt was occurring on 12 October; winter pelage was present on the rump and flanks. On 15 October, another individual had about one-half of its posterior back covered with new pelage, and one on 12 October had the whole body covered with short, new pelage (Howell, 1929).

The feet are long and slender, and the toes are clawed and adapted for climbing rather than extensive digging. The pollex is diminutive and lacks a claw, but is functional. The smallest seeds are held within a groove in the pad at the base of the pollex and are manipulated by its muscles as the incisors remove the seed coats (Larson, 1981).

Merriam's chipmunk can run up the vertical sides of granite cliffs (Jaeger, 1929). It runs on its toes; rarely on the soles of its feet. *T. merriami* regularly ascends to heights of 7.5–24.0 m, and can travel long distances over interlocking branches of trees (Larson, 1981).

The tail of *T. merriami* usually is >80% of length of head and body (Ingles, 1965); elevation and length of tail are negatively correlated. Length of tail apparently has some adaptive significance,

and the correlation with elevation suggests that the tail is involved in thermoregulation. *T. merriami* has the bushiest tail of any *Tamias*. The tail also may be important in balance, climbing, and insulation (Callahan, 1976). *T. merriami* appears to have muscular control of its tail from base to tip (Larson, 1981).

Tamias merriami tends to lower its eyelids in bright sunlight and to close the eyes in repeated and prolonged blinks. At rest, it may tolerate strong sunlight for a few minutes with the eyelids lowered; the pupil of the eye appears as a horizontal slit. In deep shadows, eyelids are drawn so that the eye appears almost circular (Larson, 1986).

As in all members of the subgenus *Neotamias*, the dental formula is $i\ 1/1$, $c\ 0/0$, $p\ 2/1$, $m\ 3/3$, total 22 (Howell, 1929; Ingles, 1965). The hypohyal of the hyoid of *T. m. pricei* is wide and thin, whereas that of *T. m. merriami* from 400 km to the southeast is narrower and elliptical in cross-section. Another 240 km to the southeast, the hypohyal is narrower and thicker, with a cross-section approximating a fat ellipse; this is in the region of sympatry with *T. obscurus*, which has the same hyoid structure (Callahan, 1976).

Internal body temperature is 37°C at ambient temperatures of 5–30°C and rises with higher ambient temperatures (Wunder, 1970a). External body temperature usually ranges from 34 to 42°C, but varies with age, season, hour, and activity. Temperatures of adult males tend to be lower than those of adult females. Young-of-the-year males have lowest temperatures in January. Body temperature is lower when an individual first emerges from its night shelter, temperature increases during morning foraging, midday temperatures are less than those in morning, and temperature when *T. merriami* returns to the night shelter is lower than earlier in the day. High body temperatures of 40–42°C occur in females 7–10 days preceding the opening of the vulva, and temperatures of males and females are similar only in the breeding period. Temperatures of adult females reach an afternoon peak at 1600–1700 h, whereas those of adult males reach their peak at 1500–1600 h (Larson, 1981).

Heat lost by evaporation increases as ambient temperature increases, but it is never >60–70% of heat produced by metabolism. Minimal thermal conductance at 15–25°C is 0.55 calories $g^{-1} h^{-1} ^\circ C^{-1}$, but at 5°C thermal conductance is reduced by 20%. At a given ambient temperature, thermal conductance is greater during activity than when at rest (Wunder, 1969).

Minimal oxygen consumption of 1.05 cm^3 of oxygen $g^{-1} h^{-1}$ occurs at an ambient temperature of ca. 30°C (Wunder, 1969). Oxygen consumption increases with running velocity at a given ambient temperature to maximum levels that are dependent upon ambient temperature (Wunder, 1970b). Lack of drinking water does not affect oxygen consumption (Wunder, 1970a).

Resting heart rate decreases with increasing ambient temperature to ca. 25°C, but does not vary significantly at ambient temperatures of 25–37.5°C. When water is unavailable, heart rate decreases ca. 25%; this decrease is associated with the resulting reduction in body mass (Wunder, 1969).

In captivity, *T. merriami* is less active when rations of water are minimal than when water is provided ad lib. Feeding activity seems to be confined to a short time in the morning after the daily ration of water. Another consequence of reduction in drinking water is that chipmunks spend less time grooming and their pelage becomes dirty and oily (Wunder, 1970a). *T. merriami* drinks water equal to ca. 12% of its body mass/day, but can reduce this to 1.5% when water is unavailable; i.e., mass may decrease 23% and body temperature remains unchanged. Water lost by evaporation is reduced ca. 46% at 37.5°C. Thus, *T. merriami* can effect a savings in water lost by evaporation in response to lack of water. When running (20 m/min at ambient temperatures of 15, 30, and 35°C), water lost by evaporation increases 5–7.5 times over resting levels (Wunder, 1969).

While running, salivation occurs at 35°C (Wunder, 1968). At ambient temperatures of 35–37.5°C, *T. merriami* assumes a prone position with limbs extended, but does not salivate. When exposed to temperatures of 40°C, it salivates, but only the chin and nose are wet. At $\geq 35^\circ C$, *T. merriami* is inactive, but at temperatures of ca. 5°C it is restless (Wunder, 1970a).

Averages and ranges of measurements (in mm) of the baubellum are: length of base, 0.38 (0.26–0.42); length of shaft, 0.66 (0.59–0.85); depth of shaft, 0.21 (0.20–0.29); length of tip, 0.51 (0.39–0.59); length of keel, 0.22 (0.29–0.26); angle of the tip-shaft, 154°

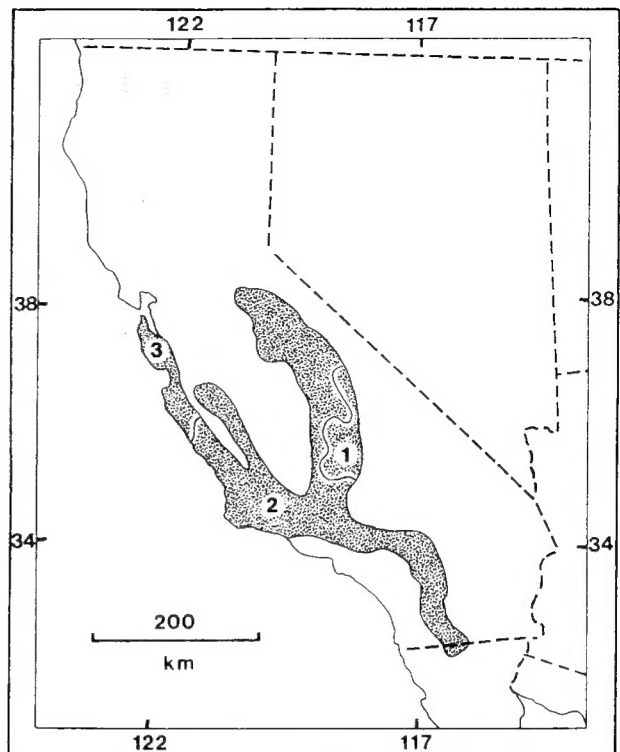


FIG. 4. Distribution of *Tamias merriami* in California and Baja California (Hall, 1981): 1, *T. m. kernensis*; 2, *T. m. merriami*; 3, *T. m. pricei*.

(150–162°). The base and shaft of the baubellum have a continuous curve and an obtuse angle without a specific apex and with a wide open U-shaped base-shaft form. The base is about as deep as the shaft, with no taper toward the rounded proximal end. The tip-shaft angle is large and has an inconspicuous heel. The tip is relatively short, with a prominent medium-sized keel and narrow flanges that do not extend onto the shaft. The tip is straight with no lateral bend and no counterclockwise twist (Sutton, 1982).

The shaft of the baculum is thin, with a low keel that extends 40% of the length of tip. The tip is 16% of length of shaft, the angle formed by the tip and shaft is 130°, the distal 10% of the shaft is compressed laterally, the base is incised dorsally, and the shaft is ca. 4.88 mm in length (White, 1953).

In one male, the maximum length of organs in the right scrotal sac was 35.2 by 11.8 mm on 18 March. Length and width of scrotal organs (in mm), respectively, were: 2 December, 15.1, 7.8; 21 December, 22.7, 8.0; 19 January, 26.3, 10.5; 22 February, 26.5, 10.8; 7 April, 25.0, 10.0; 4 May, 23.5, 8.5; 18 May, 9.2, 8.7; testicular quiescence occurs for ca. 75 days in June to August (Larson, 1981).

ONTOGENY AND REPRODUCTION. Males may be in breeding condition throughout the year. However, most males are in breeding condition from December through May, with a peak in February and March (Larson, 1981). In the San Bernardino Mountains, an estrous female and a male with mature sperm in the epididymides were present on 15–16 March (Callahan, 1976, in litt.). Gestation is ca. 32 days and 9–10 weeks elapse between copulation and time that young-of-the-year become active outside the nest chamber (Larson, 1987).

At lower altitudes, young are born by May or earlier, but at higher elevations young may be born in July (Storer and Usinger, 1963). About 32 days elapse between birth of the young and their emergence. At Palo Escrito, Monterey Co., young appeared from 21 March to 2 October, but usually was from late March to late May (Larson, 1987). Size of litters usually is three to six (Storer and Usinger, 1963). At Palo Escrito, litter size (based upon number of active juveniles) was: 1, 3% of litters; 2, 14%; 3, 5%; 4, 64%, 5, 14% (Larson, 1987). In the San Bernardino Mountains, lactating

females were observed from 8 to 24 June, and at Sugarloaf Mountain on 28 May (Callahan, 1976, in litt.), and three one-third-grown young were found in a rotten stump on 16 June. After that date, many young-of-the-year were present (Grinnell, 1908).

Softly uttered mewling notes are emitted while young are in the nest chamber. Visual, auditory, tactile, and olfactory senses are functional at the time young chipmunks become active at the entrance to the nest chamber. Alarm and agitation notes are given from the 1st day out of the nest chamber (Larson, 1981).

Young become active outside the nest chamber at ca. 1 month of age (Storer and Usinger, 1963). At emergence from the nest chamber, there are no differences in mass between sexes (ca. 15–18 g). However, within a few days mass of young females begins to exceed that of young males, and this trend continues. By the time young have been abroad 3 weeks, their rapid growth is over. In some years, young may reach the mass of adults as early as their 6th week of independent activity. By the 11th week of independence, subadults cannot be distinguished in size from adults, but age groups can be characterized by pelages and genitalia. Intensive foraging characterizes the activities of juveniles. In this period, wariness is at its lowest point in the life history. Immature females first show open vulvas (16 weeks after birth) when they have achieved 90% of adult mass. Thereafter, growth slows and further changes in body mass chiefly are expressions of daily and seasonal activities. By late November, neither subadult males nor females are distinguishable from adults on the basis of mass, but pelages are distinct (Larson, 1981).

Coloration of young resembles that of adults in May, but flanks of young are more rufous, and the dorsal stripes are better defined and stronger, the outer pale stripes being nearly white. However, juvenile pelage is fine and soft, in contrast to the coarser pelage of adults (Allen, 1890).

Muscular coordination is weakly developed in juveniles; e.g., they descend a tree backwards, not head first. Accuracy in jumping develops within the first 2 weeks. As the young travel over limbs above the ground they frequently fall without injury or broken bones. The muscular pads of the feet may not be sufficiently developed to grip rough substrates (Larson, 1981).

As mother and young forage, she communicates with them by call and by stance; the young respond according to the kind of behavior she is exhibiting. The reaction of young to the sharp alarm note of the adult is to cease motion instantly. In this early learning period, the young react to responses of the adult and not directly to the source of danger. Generally, young follow a sequence of behavioral development; exploration in the area around the shelter entrance, tandem following, trail recognition, food-source recognition, wariness in response to the mother's expressions, play, exploration of the environment in an ever-widening arc, expression of rank order and dominance roles for individuals of each sex, voracious feeding, convergence patterns at night-shelter sites, and entrance order that follows a pattern of rank (Larson, 1981).

By their behavior, juveniles indicate that skin glands (cheek, chin, and shoulder) are active at 4 weeks of age. The reception of scent from the anal glands (located internally, immediately anterior to the anal sphincter, and ring-like) becomes pronounced before testes have descended into the scrotum. Secretions from the genital lips of females indicate glandular activity and serve as stimuli to which males and females respond. Parotid glands of subadult males enlarge in early winter in advance of their breeding and remain swollen until molt begins. This gives males the unique appearance of a short, broad face when compared with the narrow crown-rostrum dimensions of the face of females. During their 1st year, the percentages of males with scrotal testes are: August, 12; September, 37; October, 58; November, 81 (Larson, 1981).

External changes during growth and development of males are, in order of appearance: swelling and pigmentation of penial sheath; freeing of scrotal sac from abdominal wall; descent of testes from abdominal cavity; gradual enlargement of testes within the scrotum until they become pendulous; dark pigmentation of scrotum; bulging of cauda-epididymis; swelling of bulbourethral glands at base of tail; swelling of parotid gland at angle of each jaw. External changes during growth and development of females are, in order of appearance: an unfurred circular area appears that surrounds the genital lips and becomes darkly pigmented; genital lips swell slowly and become vascularized (skin color changes from white to pink to purple gray to deep red); hyaline membrane that covers vulva ruptures; vulva opens and fertile copulations may take place; subsidence of

swelling of genital lips; vulva closes and remains visible as a pit-like depression in the median furrow; inactivity; recurrence of genital activity and opening of vulva at regular intervals of ca. 70 days (Larson, 1981).

In juvenile and immature females, the position of the vulva is indeterminate. The vulva is closed and a tight membrane of thin tissue encloses it; the median line is indistinguishable. The anal-genital distance is ca. 3 mm. The skin of the genital region is white or pale gray. Puberty is characterized by pinkness of the skin, swelling of lips of the vulva, appearance of the median line as a slight furrow, and rupture of the covering membrane (Larson, 1987).

In December–February, a marked swelling of the external genital region develops in subadult females. As a result of this swelling, the median line becomes a deep furrow and the position of the vulva clearly shows a pit-like depression along the median line. Pre-courtship chases begin, even though effective insemination may not take place for another 6–8 weeks. Presence of dried blood in the genital area near or on the median line is a reliable indicator of a recently opened vulva. The skin of the genital region changes from a deep rosy pink to darkly pigmented, and a circular hairless area surrounds the vulva as courtship progresses. After copulation, the vaginal walls are everted so that the vulva is an opening at the distal end of a cylindrical, pendulous structure. In one female, this structure was 3.5 by 3.5 mm. During pregnancy, the median line is distinct and the vulva is open (Larson, 1987).

By the time a female completes molt from juvenile to subadult pelage, the mammae are pin-head size (Larson, 1981). Nipples of subadults become button-like; nipples of adults are elongate, slender, and pointed. The skin of the mammary gland area is white. In early pregnancy, the nipples have darkly pigmented tips; in late pregnancy, nipples are swollen, pink, and full. It is impossible to distinguish nipples during pregnancy from nipples during lactation, but as nipples sink into their bases, which are crater-like, two folds usually are apparent; immediately after lactation, these folds are not present. During lactation, nipples are swollen and full. The skin of the nipple and mammary gland is rosy pink. Each nipple is situated on an enlarged conical mound of the mammary gland, which is hairless. There is a single or double fold at the base of each nipple. The vulva is closed, the skin of the genital area is white, and the median line is a shallow furrow (Larson, 1987).

Involution may come at the close of the normal completion of the cycle of growth and development of the young; interrupted lactation may occur with premature loss of the litter. At the close of the weaning period, the adult female has a closed vulva, the skin of the genital region is white, and the nipples are collapsed. The median line is indistinct and the position of the vulva is apparent as a slight pit-like depression. In interrupted lactation, the vulva is open, the vaginal walls are everted, and only the nipples show involution, suggesting that pregnancy may occur immediately after loss of a litter. In involution, the tips of the nipples become dry and brown; these dried tips may be brushed off (Larson, 1987).

Merriam's chipmunk can live to 5 years of age in the wild (Larson, 1987). One animal showed no significant changes in mass from subadulthood to 5 years of age (Larson, 1981).

ECOLOGY. *Tamias merriami* occupies habitats with a wide range of climate (Larson, 1981). It occurs in habitats with trees, shrubs, logs, stumps, snags, rocks, and litter (Barrett et al., 1980). The habitat principally is brush, as in extensive chaparral-covered (Adenostoma, Arctostaphylos, Quercus) slopes mixed with oak (Quercus) and pine (Pinus) forests, or thickets along streambanks and around rock outcroppings. In the absence of competing species over most of its range, *T. merriami* enters a wide variety of habitats. It occurs in association with ceanothus (*Ceanothus*) and manzanita (*Arctostaphylos*) of several species, blue oak (*Quercus douglasii*), black oak (*Q. kelloggii*), digger pine (*P. sabiniana*), bigcone pine (*P. coulteri*), bigcone spruce (*Pseudotsuga macrocarpa*), lodgepole pine (*P. contorta*), single-leaf pinyon, and juniper (*Juniperus*—Johnson, 1943). In Ventura Co., California, *T. merriami* lives in an area where summer air temperatures of 30–35°C are common, whereas during winter the area experiences frequent freezing temperatures and often is snow-covered (Wunder, 1970a).

At lower elevations on the western slope of the Sierra Nevada, *T. merriami* inhabits areas of chaparral mixed with small trees; it chiefly lives at <1,200 m elev. and forages in brush (Sumner and Dixon, 1953). In the San Bernardino Mountains, it is common in mingled scrub (*Quercus dumosa*) and golden oaks (*Q. chrysolepis*)

on the Pacific slope of the mountains down to 900 m elev. *T. merriami* also occurs in the black oak belt up to 2,100 m elev. (Grinnell, 1908). In the San Gabriel Mountains, the lower limit of the range of *T. merriami* on the coastal face of the mountains is roughly coincident with that of manzanita; i.e., the distribution of *T. merriami* begins in the main belt of chaparral above the lower foothills. It seems to reach maximum abundance amid granite talus, scrub oak, and Douglas fir (*Pseudotsuga menziesii*) at the upper edge of the chaparral association, but *T. merriami* is absent from all but the lower fringe of the ponderosa pine (*Pinus ponderosa*) forest. On the desert slope, it occurs in rocky areas in the single-leaf pinyon-juniper association, but also is in the black oak woods (Vaughan, 1954). In the San Jacinto Mountains, *T. merriami* occurs in chaparral habitat. Though common on brush-covered hills, it was never seen in clumps of timber scattered in the sagebrush (*Artemisia*) of valley areas (Grinnell and Swarth, 1913). Merriam's chipmunk is abundant around Mount Pinos from 1,500 to 1,800 m elev. in scrub oak and single-leaf pinyon forest. In early October, *T. merriami* was observed gathering nuts of single-leaf pinyon; the ground at bases of trees was covered with heaps of cone scales from which radiated the trails of chipmunks. Near Fort Tejon, which is below the single-leaf pinyon belt, *T. merriami* was more scarce and confined to thickets of scrub and golden oaks (Elliot, 1904). At Palo Escrito, *T. merriami* inhabits groves of valley oaks (*Q. lobata*) that occur in pure and mixed stands. It occasionally enters dense stands of chaparral (Larson, 1986).

When acorns of valley oaks are in short supply, fruits of interior live oak (*Q. wislizenii*) and those of scrub oak are used, but acorns of blue oak are not gathered (Larson, 1986). Merriam's chipmunk is known to consume >70 species of plants, but acorns are a source of food throughout the year (Larson, 1981). Valley oaks serve as a source of acorns, flowers, buds, and insects. Other foods are arroyo willow (*Salix lasiolepis*), red willow (*S. laevigata*), valley oak, live oak (*Q. agrifolia*), golden oak, scrub oak, California laurel (*Umbellularia californica*), gooseberry (*Ribes*), western sycamore (*Platanus racemosa*), California rose (*Rosa californica*), chamise (*Adenostoma fasciculatum*), blackberry (*Rubus ursinus*), poison oak (*Rhus diversiloba*), hollyleaf redberry (*Rhamnus crocea*), coffeeberry (*Rhamnus californica*), ceanothus (*Ceanothus ramulosus*), manzanita, sticky monkeyflower (*Diplacus*), elderberry (*Sambucus coerulea*), snowberry (*Symphoricarpos rivularis*), chaparral honeysuckle (*Lonicera interrupta*), black sage (*Salvia mellifera*), miner's lettuce (*Montia perfoliata*), Indian milkweed (*Asclepias eriocarpa*), ripgutgrass (*Bromus rigidus*), hill star (*Lithophragma heterophyllum*), red-stem filaree (*Erodium cicutarium*), fungi (*Hysterangium*, *Melanogaster*, *Genea*, *Tuber*, *Delostria*), lichens, mosses (spores of *Tortula princeps*—Larson, 1986), serviceberries (*Amelanchier alnifolia*—Grinnell, 1908), juniper berries, and single-leaf pinyon nuts (Jaeger, 1929). Cheekpouches of one *T. merriami* had 20 seeds of Jeffrey pine (*P. jefferyi*), another had 1,169 mixed small seeds (Storer and Usinger, 1963), and another had eight sugar pine (*P. lambertiana*) seeds in one cheekpouch (Sumner and Dixon, 1953). Animal foods include Arachnida, Homoptera, Coleoptera (adult Cerambycidae), Diptera (larvae), Lepidoptera (larvae of Tortricidae, adult Danaidae, larvae of Diptidae), Hymenoptera (galls and larvae, Formicidae), Reptilia (western fence lizard *Sceloporus occidentalis*), Aves (embryonic membrane from egg shells of California quail *Lophortyx californica*, and muscle tissue of sparrow *Zonotrichia*). Merriam's chipmunk also eats seeds of annuals from feces of goldfinches (*Spinus*—Larson, 1986). *T. merriami* contributes to the natural reseeding of forests (Jaeger, 1929).

Changes in size of populations seem related to patterns of rainfall. Populations appear to decrease in drought years and increase in years with high rainfall (Larson, 1987).

Where *T. merriami* coexists with *T. obscurus* in southern California, zones of overlap are narrow and there is evidence of competitive exclusion (Callahan, 1976). Often, areas of sympatry are drainage areas and canyons in which the transition zone extends into the upper Sonoran zone or where topography is such that a mosaic pattern of vegetation is formed. *T. merriami* and *T. obscurus* are sympatric in the San Bernardino and San Jacinto mountains. Presence of *T. merriami* in areas of allopatry is correlated with density, crown cover, and basal area of western coniferous forest vegetation. *T. merriami* is associated with presence of white fir (*Abies concolor*), buckwheat (*Eriogonum fasciculatum*), black oak, and willow (*Salix*), and with absence of single-leaf pinyon. When sympatric with *T. obscurus*, the presence of *T. merriami* is correlated

with density, crown cover, and basal area of single-leaf pinyon trees. Vegetation associated with *T. merriami* in sympatric sites is similar to that associated with *T. obscurus* in allopatric sites (Blankenship, 1985). On the Pacific slope of the San Bernardino Mountains, where *T. obscurus* does not occur, *T. merriami* occupies both upper Sonoran (*Q. kelloggii*–*P. coulteri*) and transition zones. In the San Bernardino Mountains, *T. merriami* and *T. obscurus* meet just north of Big Bear Lake at ca. 2,100 m elev., where upper Sonoran single-leaf pinyon-juniper woodland occupied exclusively by *T. obscurus* gives way to ponderosa pine and white fir, which characterize the transition life zone. These species also meet on the desert slope of Sugarloaf Mountain in the vicinity of Wildhorse Meadow (2,550–2,580 m elev.—Callahan, 1976). Thomas Mountain (2,075 m elev.) was thought to be occupied exclusively by *T. merriami* (Callahan, 1977), but *T. obscurus* recently has expanded its range to include this mountain (Davis and Callahan, 1992). *T. merriami* is the only chipmunk in the mountains of San Diego Co., except around Jacumba and Mountain Spring on the east slope, where *T. obscurus* occurs (Callahan, 1976).

In the San Bernardino Mountains, *T. obscurus* occupies the single-leaf pinyon-juniper belt below *T. merriami*. In the San Jacinto Mountains, *T. obscurus* occupies the transition life zone above *T. merriami* (Callahan, 1976). In the San Jacinto Mountains, *T. merriami* largely is restricted to chaparral associated with oak-pine woodland. In the foothills south of Banning, the species is common in arid chaparral with scattered live oaks. On San Jacinto Peak at elevations >1,650 m, it is replaced by *T. obscurus*, a reversal of the zonation found in the San Bernardino Mountains (Callahan, 1976).

The burrow serves for escape shelter, sleeping, rearing young, and in higher elevations for hibernation. Burrows usually are hidden in decaying stumps (Storer and Usinger, 1963), hollow trees, or under fallen logs (Jaeger, 1929). In Santa Cruz Co. on 24 June, two nests were found in dead snags of broken-off ponderosa pines on a sandy slope covered with chaparral and a few cypress trees (*Cupressus*). One nest was a simple depression lined with soft and finely crumbled dead wood and shredded bark in a cavity 18 cm in diameter 5 m aboveground. A second was at a height of 13 m in a crevice at the top of a large truncated ponderosa pine. Two chipmunks entered each tree nest at 2010–2020 h, well after sunset (Broadbooks, 1977). Merriam's chipmunk also may occupy abandoned dens of *Neotoma fuscipes* (Callahan and Estep, 1982; Elliot, 1904; Jaeger, 1929). A burrow occupied by two juveniles was dug in hard, rocky soil and seemed too extensive to be the work of chipmunks, resembling instead the burrows of *Spermophilus* (Callahan and Estep, 1982).

Burrow systems include short side branches that may be used as turnaround points or as places for deposition of fecal pellets. One nest, located in a woodrat den, was composed of 95% rotten wood plus plant fibers and leaves, and was 700 cm³ in volume. The nest was a solid mass of plant fibers that were prepared by drawing a piece of dead root or stem between the teeth so that the outer layer curled up and accumulated at one side of the mouth. The chipmunk also loosens fibers by gnawing, then strips it away from the root or stem. Pine straw, leaves, and similar nest materials apparently are used without modification (Callahan and Estep, 1982). One nest was located inside a log. It contained ca. 2 l of mulch of finely divided, dry, leaves of valley oak with bits of dry moss. A cup-like depression 6.4 cm in diameter, apparently the nest, was located on one side of the mulch (Larson, 1986).

Nest chambers may be in underground tunnels or cavities and woodpecker holes in valley oaks (Larson, 1981). Usually, young are reared in cavities in trees. These cavities are at heights of 3.6–19.5 m aboveground in red willows, western sycamores, and valley oaks (Larson, 1987).

Merriam's chipmunk may be killed by fires (Jaeger, 1929) or predators including gray foxes (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), badgers (*Taxidea taxus*), weasels (*Mustela*), sharp-shinned hawks (*Accipiter striatus*), Cooper's hawks (*Accipiter cooperii*), great horned owls (*Bubo virginiana*), Pacific rattlesnakes (*Crotalus viridis*), garter snakes (*Thamnophis*), and gopher snakes (*Pituophis melanoleucus*—Larson, 1987). A calling female was dived upon by a sharp-shinned hawk, but the predation attempt was not successful (Callahan, 1981). *T. merriami* has been exhibited in zoos (Dolan and Moran, 1969).

Plague (*Yersinia pestis*) has been detected repeatedly in Merriam's chipmunk (Nelson, 1980). Endoparasites include the coccidia

ans *Eimeria dorsalis* and *E. tamiasciuri* (Hill and Duszynski, 1986), the nematode *Syphacia*, the cestodes *Taenia* and *Dipylidium*, and the fungus *Haplosporangium*. Ectoparasites include the mites *Hae-molaelaps glasgowii* (Larson, 1987), *Trombicula dinehartae* (Brennan and Jones, 1954), and *Spinolaelaps* (recovered from a nest—Callahan and Estep, 1982), the ticks *Dermacentor occidentalis* and *Ixodes sculptus* (Cooley and Kohls, 1945; Furman and Loomis, 1984), the lice *Hoplopleura arboricola* (Ferris, 1916, 1951) and *Neophaematopinus pacificus* (Larson, 1987), the fleas *Cediopsylla inaequalis*, *Hoplopyllus anomalus*, *H. foxi*, *Atyphloceras multidentatus*, *Hystriochopsylla*, *Rectofrontia fraterna*, *Carteretta carteri*, *Odontopsyllus dentatus*, *Diamanus montanus*, *Malariaeus telchinum*, *Monopsyllus fornacis* (Linsdale and Davis, 1956), *Anomiopsyllus falsicalifornicus* (Barnes et al., 1977), and *Ceratophyllus ciliatus* (Traub et al., 1983), and the dipteran *Cuterebra* (Larson, 1987).

Tamias merriami receives body injuries in the course of daily and seasonal activities. Injuries occur more often to ears than to tails. Males have about twice as many ear injuries as females, but injuries to females involve more tail than ear injuries. Ear injuries may be a shallow nick, multiple nicks, jagged gouges, slits, awl-shaped perforations, or removal of an entire pinna with jagged scar tissue remaining. Broken tails frequently occur and do not influence survival. Breaks in tails usually are located distal to the mid-region. When a break occurs near the terminus of the tail vertebrae, replacement follows. When 25–33% of the tail vertebrae are missing, marginal hairs show rapid growth and are redirected to form a terminal brush; this restored tail is about its original length. With a mid-region break, a knob-like growth forms and the stub remains (Larson, 1987).

BEHAVIOR. Merriam's chipmunk is diurnal (Wunder, 1970a), and throughout much of its range it is active in winter and does not hibernate. However, at the upper edge of its elevational range, it may hibernate when the weather is snowy and cold (Sumner and Dixon, 1953).

There are four major activity periods in the year. In autumn, activities include increased mobility, intensive feeding, harvesting and caching, increased aggressive chases, choosing a shelter site, decrease in hours abroad, and autumnal quiescence. Winter activities include emergence from autumnal quiescence, pit digging, concentration of males into groups, high levels of male-male tolerance, marking trails, precourtship, courtship, male display, copulation, and gestation. In spring, activities include arrival of wanderers, continued mating, courtship chases, copulations, gestation, gathering of nesting materials, parturition, rearing of young, postpartum heat, transfer of young, independent activity of young, and decreased activity of adult males. In summer, litter mates no longer travel together, adults molt and gain body mass, mobility of adults begins, there is summer quiescence, young females mature, and dispersal of young begins (Larson, 1981).

The two daily foraging intervals are separated by a midday rest. In midsummer, the first foraging period spans ca. 3.5 h of continuous activity by adults and a longer period for nonadults. The second period occurs in midafternoon and ends when the chipmunk, on its return journey, abruptly ceases searching for food and makes the final rush to its night shelter. Foraging in the afternoon is done in a more leisurely manner than in the early morning. Foraging areas are used communally; individuals do not forage out of range of communication with conspecifics. Directional orientation and spacing at a communal foraging ground is subject to constant shifting of positions by individuals. Juveniles foraging as litter mates are mutually tolerant at a distance of 20–25 cm; at a distance of 5 cm, repositioning occurs. Older chipmunks do not tolerate spacing <2.4 m unless an intervening log or foliage separates the two. Thus, at foraging grounds many short chases occur to maintain distance. There is no evidence that these chases are for purposes other than immediate spacing. Seldom is there conflict over possession of food (Larson, 1981).

Apparently, *T. merriami* is dependent on woodpecker cavities in trees, on natural cavities, and on burrows dug by pocket gophers (*Thomomys*) for night shelters (Larson, 1986). Juveniles disperse widely and explore virtually any existing pocket gopher burrow, hollow tree, or other natural cavity, apparently establishing temporary residences therein. Such exploratory behavior likely accounts for the wide range of dens used by Merriam's chipmunk (Callahan and Estep, 1982).

Of 129 night shelters, 127 faced east or within 30° of east; of the exceptions, one faced west and one faced north, but had three entrances in the same log that faced eastward. Locations of night shelters were in (in percent): living trees, 52; fallen logs, 23; dead snags, 14; ground, 9; abandoned bird nest, 1; woodrat den, 1. Of shelters located in trees, logs, and snags, 85% were in valley oaks, 7% in western sycamores, 4% in red willows, 1% in golden oaks, and 1% in arroyo willows. Two-thirds of entrances in trees, logs, and snags were natural openings and one-third were woodpecker holes. Locations aboveground were at heights of 21.6 cm–19.5 m; 70% were >3 m aboveground. These night shelters are relatively permanent; of 120 in trees, logs, and snags, all but five were still in use after 8 years. Of these five, three were felled by wind, one was destroyed by weathering and fungi, and one was broken by cattle using the log as a rubbing post. One night shelter, which housed seven individuals, was in a dead tree and measured 20.3 cm deep and 10.2 cm in diameter. At night no part of the chipmunks' bodies was visible above the level of the entrance. Apparently, the seven bunched closely at the bottom of this cavity (Larson, 1986).

Rarely does Merriam's chipmunk go >300 m from the night shelter. The distance traveled depends upon foraging areas; thus, there is seasonal variation in distance moved during the day. *T. merriami* begins its early morning foraging at sites located ≥18 m from the night shelter, and then moves upslope as it forages. One foraging site was 397.5 m from the night shelter. In spring and summer, ca. 92% of diurnal activity occurs at the foraging ground. Its daily food gathering often takes *T. merriami* into chaparral that extends into oak woodlands or grows in adjacent communities. Night shelters are not located in chaparral shrubs; rather, *T. merriami* returns in late afternoon to oak woodlands (Larson, 1986).

When active, *T. merriami* continuously moves about foraging in the underbrush (Wunder, 1970b) and regularly climbs trees (Johnson, 1943; Larson, 1981; Sumner and Dixon, 1953). Much of its activity is devoted to finding food to store. It has a pair of thin internal cheekpouches used to carry seeds, nuts, and berries (Storer and Usinger, 1963). Manipulation of food at the foraging site involves searching, locating, gathering, eating, and pouching. Grasses or green seeds usually are eaten at the foraging site. Mature seeds are carried in the cheekpouches to an extracting site, where the husks are removed and the seeds are eaten. Caching is the most common means of storage. Acorns are cached singly, usually without removal of husks, in individual pits ca. 3.8 cm deep. Each pit is covered with soil and leaf litter. These caches are patted with the forefeet moving alternately. Some foods are tucked into crevices in dead logs, between limbs, and in crotches of living trees. When acorns fall from valley oaks in autumn, chipmunks congregate beneath the trees. Upon hearing an acorn strike the ground or a log, a chipmunk rushes to the spot, locates the acorn, and picks it up in the mouth. Males and females store acorns, but females carry acorns ca. 12–48 m; ca. 2–2.5 times as far as males take them for caching (Larson, 1986).

Tamias merriami travels in chaparral by way of interconnecting branches. Shrubs are spaced such that branches intermingle and ground travel seldom is necessary. Elsewhere, Merriam's chipmunk shows a preference for logs as trailways. Low light intensity is a factor that reduces use of the ground surface for trails; logs reflect less light than does the surface of the ground. Charred logs with blackened surfaces that absorb light are used as trails when available. Merriam's chipmunk uses communal trails, with parallel segments. Seldom are alternate trails parallel for >9 m. The three routes between any two points in a trail system include a direct path with alternate circuitous paths, frequently one to the right and the other to the left. Trail convergences are numerous and may occur at intervals of 9–18 m. Trails remain in continuous use generation after generation with little alteration, except to compensate for environmental changes. When occupancy is interrupted for up to 5 years, a new generation of chipmunks will reestablish travel essentially over the same routes. Living branches are used as parts of trails more often than are dead branches (Larson, 1986).

Use of trails varies seasonally. In winter, after deciduous trees have dropped their leaves, *T. merriami* no longer travels over high-level trails by way of limbs. Instead, it travels over parallel pathways at ground level or over logs within 1 m of ground. By April, when new foliage appears, it begins to use trails that lead through trees and high branches (Larson, 1986).

Tamias merriami uses a variety of pausing sites during its movements that include: dead twigs or limbs (1.3–5.1 cm in di-

ameter), 75% of the time; living limbs (0.6–20.3 cm), 10%; ledges (tree trunks, exposed roots), 10%; irregular surfaces on rocks (5.1 cm in diameter) and fallen logs (5.1–152.4 cm in diameter), 5%. Merriam's chipmunk pauses for observations beneath canopy in preference to open sky, and usually behind foliage. When *T. merriami* ascends a tree trunk to observe, it may pause to look about, but often it travels to a lateral branch, then pauses, stands upright with its back to the trunk, and looks about, or enters foliage and crouches (Larson, 1986).

Merriam's chipmunk also has resting stations. To relax, it may flatten its body so that its venter is in contact with the substrate, or it may crouch or stand partly upright as it rests. There is a long rest between morning and afternoon foraging times. Rest areas are located in the vicinity of the foraging area and may be on logs, twigs, or limbs beneath canopy, often at heights of 13.5 m above-ground. The eyelids may be lowered to slits and the pinnae may be drawn downward; it is silent and is not easily aroused to move or to vocalize (Larson, 1986). Often, the tail hangs downward and sways in a breeze. Muscle stretching at the end of a rest period is common (Larson, 1981).

The tail usually is carried over the back (Jaeger, 1929). *T. merriami* may move its uplifted tail in a slow, serpentine waving motion. It may sit in shade for ≥ 30 min performing these movements, which apparently are accompanied by piloerection of the tail; possibly it is dumping heat (Callahan, 1976). Tail movements also include rapid switching, jerks, slow undulations, and rhythmic wavings forward then back. Body language is expressed in stance, rigid extensions of the neck, elevations of hips, positions of crouching, degrees of upright standing, and choice of substrates for observational surveys. Deposition of scent from the feet occurs as *T. merriami* traverses trails. Oiliness of footprints has been shown by prints on paper (Larson, 1986).

The number of hours each day that *T. merriami* is away from its night shelter is related to times of sunrise and sunset. It often exits the night shelter suddenly, bounding out and immediately moving away from the entrance (Larson, 1981). Merriam's chipmunk emerges from its night shelter ca. 40 min before direct sunlight strikes the entrance. However, it may pause on a ledge near the night shelter before the initial descent for the day and stand in full sunshine while it grooms. At rest, it may allow direct sunshine to reach the body, but not the eyes, for 20 s–3 min. In months when the average amount of light is > 240 footcandles, *T. merriami* moves into areas with filtered sunlight, then into shadows. This movement away from light is independent of air temperature. Whereas it may run across ground in direct sunlight > 400 footcandles, at no time does it remain there. Merriam's chipmunk may tolerate a 3-s exposure to this high illumination, but no more. From October to April it does not seek shadows as it forages; activities are carried out in filtered sunlight as often as in direct sunlight as it moves beneath leafless branches (Larson, 1986).

Sources of water for Merriam's chipmunk include streams, springs, reservoirs, cattle troughs, hollows in limbs and trunks, and sap of oak trees (Larson, 1986). After rains, shallow pockets on top of rocks also provide water (Jaeger, 1929). Acorns of valley oaks contain ca. 43% water. In years when acorns are not available, *T. merriami* makes much greater use of water in cattle troughs. In drinking from troughs and quiet pools, it takes in water by suction and the head is not elevated for swallowing. It drinks from running water by first aligning itself to face upstream, and laps against the moving current. The tongue is extended and the tip curves upward and inward as it laps rapidly. When Merriam's chipmunk gets wet, it may dry itself by plowing its way forward and downward through the soft soil of a pocket gopher mound (Larson, 1986).

There is no evidence that light rain alters the daily activities of *T. merriami*, but it will cease foraging during heavy rains and may enter its night shelter. After snowfall, Merriam's chipmunk may run across the frozen crust of snow. In March, it was active during a sleet shower, and in April, mild hail storms did not reduce foraging activities. Heavy frosts may cause *T. merriami* to become active ca. 2 h later in morning. Preceding a storm, accompanied by falling barometric pressure, chipmunks frequently show bursts of activity, but preceding one storm when the barometric reading reached 3.05 cm below standard all activity stopped. Overcast skies do not influence activity. Fog may cause Merriam's chipmunk to remain active longer in the morning or to become active later in the morning, but dense fog may cause it to seek night shelters. *T. merriami* will tolerate air moisture content as low as 22%, but seeks rest stations

where air moisture content is 37–42%. It tolerates air temperatures of -2.2 – 33.3°C . However at 32.2°C , heat limits its activity. Appearance is affected by temperature: -2.2 – 5.0°C , fluff out pelage, hairs held at right angles to the body, pads of feet are contracted; 13.9 – 16.1°C , hold hairs at acute angles of ca. 80° ; 18.3 – 25.5°C , hold hairs at acute angles of ca. 40° ; 26.6 – 33.3°C , hold hair against body so that body appears slick and without pelage, pads are moist; 29.4°C , activity markedly diminished, animals are lethargic; 31.1°C , 90% of chipmunks are inactive in rest stations with cover of foliage; 32.2°C , adults are immobilized; 33.3°C , immatures are prostrate, activity is extremely limited; 35.0 – 38.9°C , not active (Larson, 1986).

Merriam's chipmunk is not active in moderate and heavy winds. When it manipulates food, it stands upright on its hind feet with its back to the wind, but most frequently with the trunk of a tree or branch intervening. As it pauses to observe, manipulate food, or relax, it allows the tail to hang downward. Often, wind blows the tail freely to and fro. In this manner, the tail and widely spaced hairs resemble a leaf blowing in the wind. Under these circumstances, wind may contribute to its concealment (Larson, 1986).

A close relationship exists between the California woodpecker (*Melanerpes formicivorus*) and Merriam's chipmunk. Acorns stored by these birds in snags and dead wood of valley oak trees frequently are extracted by chipmunks. In the attempts of woodpeckers to protect their stores, two birds fly downward in direct attack. Usually, the chipmunk spirals around the trunk and escapes (Larson, 1986).

When startled, *T. merriami* ceases to forage, runs to the nearest prominence, ascends it, looks around, and remains quiet for 3–12 min. Except during the season when territories are being established, *T. merriami* will not retreat to its night shelter in daytime (Larson, 1986).

Besides getting food and caring for young, *T. merriami* appears to play. One will pursue another around and about over logs and stumps (Storer and Usinger, 1963). Chase is a form of communication that is linked to many kinds of activities. Usually, the chase is not an expression of violence. Chases may be used to maintain spatial distance between foraging individuals, as exercise, as aggression toward strangers, as an expression of ownership rights at newly established shelter sites, as an expression of dominance and rank order at shelter sites, in precourtship, and in mating (Larson, 1981).

Calls include the chuck, chip, chipper, and trill. The chuck is given at a maximum rate of ca. 160/min, usually by a concealed individual. This call seems to cause other chipmunks to remain quiet and hidden. Rarely, a second concealed individual also may give the chuck. The chip usually is given by an exposed individual near its den. In campgrounds and other public areas, chipmunks may give the chip even when distant from their burrows. Unlike the ventriloquial chuck, which has a narrow frequency range, the chip has a wide frequency range and is easily located. Where the chuck causes other chipmunks to be quiet, the chip causes them to be noisy. Merriam's chipmunk does most of its chipping in summer, when population densities are high and lactating females remain close to their nests (Callahan, 1976).

Other calls include the trill and chipper. The trill is given by a number of other species of chipmunks, but it is particularly characteristic of *T. merriami*. It usually follows, or is interspersed with, a rapid series of chips, and is heard in situations of high-intensity alarm. The chipper, a jumbled series of notes, is given by an individual that has been startled and is racing for cover (Callahan, 1976).

There is geographic variation in calls. Average rates of calls near Columbia, Tuolumne Co., and near Green Valley Lake, San Bernardino Co., respectively, were 130 and 57 chips/min (range, 66–184 and 14–132), 1.0 and 1.1 chips/burst, and 130 and 57 bursts/min (66–184 and 5–132—Brand, 1976). Frequency ranges (in kHz) of the chip call in the San Bernardino Mountains, San Bernardino Co., San Jacinto Mountains, Riverside Co., and Columbia, Tuolumne Co., respectively, are: origin of upsweep, 1.5–3.0, 1.5–4.1, 1.0–1.5; top of upsweep, 12.5–16.0, 13.8–15.5, 11.5–15.0; bottom of downsweep, 1.5–4.0, 1.0–4.2, 1.5–3.5. Ranges in length of chips (in s) are 0.045–0.90, 0.036–0.069, and 0.045–0.085 for the three localities, respectively (Blankenship and Brand, 1987).

Although chip calls of *T. obscurus* and *T. merriami* are similar, males of these species have not been observed to approach a displaying female of the other species, even where habitats interdigitate. A male *T. merriami* sniffed at the spot where a pair of *T. obscurus* had appeared to copulate the day before, suggesting that olfactory cues may be operative at close range (Callahan, 1981).

Estrous females not only encourage pursuit and competition among males, but actively solicit aggregation of males by means of conspicuous vocal displays resembling nondirected alarm calling. The call used by females for solicitation is the same as the common alarm call, the chip, that is given by both sexes in the presence of a ground predator and inhibited in the presence of a raptor. It is an explosive, abruptly terminated, easily located call with much noise and a wide frequency range. Chip calls of estrous females tend to be produced in bursts or irregular series, rather than in the steady, rapid-fire fashion that often characterizes high-intensity, directed, alarm bouts. The vocal display is conspicuous and almost certainly entails some risk for the female (Callahan, 1981).

The female, ca. 3–5 days prior to estrus, begins to spend a great deal of time sitting on exposed perches and calls for ≥ 10 –30 min, interspersed with grooming and periods of inactivity. This behavior may occupy 3–4 h/day over several days. Males may come from distances > 200 m. They respond to the female's advertisement by approaching silently and in a hesitant, jerky manner. Upon arrival, the male sniffs the female's genital area or the perch where she has been displaying. At this stage, the female responds by moving away, sometimes uttering a faint growl if the male follows. Thus, by the time estrus begins, two to six or more males have arrived in her home range. One male gathered nest material near the female's den, perhaps establishing temporary residence during this period. Estrus lasts a few hours and largely is occupied with pursuit and male vocalization. At some point, the female stops and allows one member of the leading pack of males to mount her; usually, the successful male is one of a group of approximately equal rank at the top of the dominance hierarchy. During and after the mating chase, the female ceases to display or vocalize (Callahan, 1981).

One copulation involved a male in multiple mountings. Each included two intromissions, with a rest period of a few seconds between. In the same area, some females showed vulvas widely open with seminal overflow, indicating post-copulation. Vaginal plugs are moist, yellow, and waxy; such a plug is visible in females soon after copulation (Larson, 1981).

Following parturition, it is probable that females spend most of their time with the young for at least the first 2 weeks after birth. Females with open, jagged, purple-red vulvas have been observed, giving evidence that they are abroad shortly after birth of their litters. At least some young are transferred, probably in the 4th week after birth. Each is carried singly in the mouth of the adult female to a tree shelter. As young approach their time of emergence, the adult female becomes agitated and shows a high degree of wariness as she returns to the nest cavity (Larson, 1981).

Males that survive the breeding season often appear to be in poor condition. They return to their burrows in a bedraggled state in May, and do not reappear until August or September. They become inactive later in autumn than females, but emerge a month or so earlier in spring, perhaps because of limited opportunity to store a winter hoard. Thus, males and females spend similar percentages of the year aboveground, but harshest months are experienced by the males (Callahan, 1981).

GENETICS. *Tamias merriami* has a type B karyotype of *Tamias*. The diploid karyotype contains 38 chromosomes including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969). Based upon 20 allozymes, *T. merriami* had an average heterozygosity of 0.0662 and four polymorphic loci (serum transferrin, hemoglobin, glucose-6-phosphate dehydrogenase, and red cell phosphoglucose-tase—Levenson et al., 1985).

REMARKS. *Tamias merriami* has been placed in the *townsendii* group with *T. dorsalis*, *T. obscurus*, *T. ochrogenys*, *T. quadrimaculatus*, *T. senex*, *T. siskiyou*, *T. sonomae*, and *T. townsendii* based upon cranial and external morphology and on coloration (Howell, 1929; Johnson, 1943). Based upon bacular morphology, *T. merriami* has been placed in the *minimus* group with *T. alpinus*, *T. amoenus*, *T. dorsalis*, *T. minimus*, *T. sonomae*, and *T. townsendii* (White, 1953). Phenetic analyses of morphologic characters have grouped *T. merriami* in clusters with *T. quadrimaculatus* and *T. sonomae*. Cladistic analyses of electrophoretic data have placed *T. merriami* with *T. obscurus* and *T. palmeri* (Levenson et al., 1985; Nadler et al., 1985); based upon these analyses, *T. merriami* has

been placed in the *merriami* species group with *T. bulleri*, *T. obscurus*, and *T. palmeri* (Levenson et al., 1985).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Levenson et al., 1985; Nadler et al., 1969, 1977; Wilson and Reeder, 1993). However, there are indications that *Eutamias* and *Tamias* may be distinct genera, e.g., divergence in the late Miocene (Ellis and Maxson, 1979; Hafner, 1984), differences in pattern of dorsal stripes, structure of the hyoid, chromosomes, dental formulas, bacula (Hoffmeister, 1986), micro-complement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

Tamias is from the Greek *tamias* meaning a storer or distributor. The specific epithet *merriami* honors C. Hart Merriam, Chief of the United States Biological Survey, 1885–1910 (Jaeger, 1955).

We thank L. L. Thornton, A. M. Coffman, and other personnel in the Interlibrary Loan Department at the Auburn University R. G. Draughon Library for assistance in obtaining articles from other institutions, and K. A. Howard for preparing Fig. 4. J. R. Callahan, R. B. Forbes, and R. S. Lishak critically evaluated an early draft of the manuscript. This is journal article no. 15-923364 of the Alabama Agricultural Experiment Station.

LITERATURE CITED

- ALLEN, J. A. 1889. Notes on a collection of mammals from southern Mexico, with descriptions of new species of the genera *Sciurus*, *Tamias*, and *Sigmodon*. *Bulletin of the American Museum of Natural History*, 2:165–181.
- . 1890. A review of some of the North American ground squirrels of the genus *Tamias*. *Bulletin of the American Museum of Natural History*, 3:45–116.
- . 1895. Descriptions of new American mammals. *Bulletin of the American Museum of Natural History*, 7:327–340.
- BARNES, A. M., V. J. TIPTON, AND J. A. WILDIE. 1977. The subfamily Anomiopsyllinae (Hystriochopsyllidae: Siphonaptera). I. A revision of the genus *Anomiopsyllus* Baker. *The Great Basin Naturalist*, 37:138–206.
- BARRETT, R. H., ET AL. 1980. California wildlife and their habitats: western Sierra Nevada. United States Department of Agriculture, Forest Service, General Technical Report, PSW-37:1–439.
- BLACK, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). *Evolutionary Biology*, 6:305–322.
- BLANKENSHIP, D. J. 1985. Reproductive isolating mechanisms of southern California chipmunks: a systematic evaluation of *Tamias obscurus* Allen, 1890 and *T. merriami* Allen, 1889 (Rodentia: Sciuridae). Ph.D. dissert., Loma Linda University, Loma Linda, California, 137 pp.
- BLANKENSHIP, D. J., AND G. L. BRADLEY. 1985. Electrophoretic comparison of two southern California chipmunks (*Tamias obscurus* and *Tamias merriami*). *Bulletin of the Southern California Academy of Sciences*, 84:48–50.
- BLANKENSHIP, D. J., AND L. R. BRAND. 1987. Geographic variation in vocalizations of California chipmunks *Tamias obscurus* and *T. merriami*. *Bulletin of the Southern California Academy of Sciences*, 86:126–135.
- BRAND, L. R. 1976. The vocal repertoire of chipmunks (genus *Eutamias*) in California. *Animal Behaviour*, 24:319–335.
- BRENNAN, J. M., AND E. K. JONES. 1954. A report on the chiggers (Acarina: Trombiculidae) of the Frances Simes Hastings Natural History Reservation, Monterey County, California. *The Wasmann Journal of Biology*, 12:155–194.
- BROADBOOKS, H. E. 1977. Tree nesting and maternal behavior of chipmunks. *The Southwestern Naturalist*, 22:154–155.
- CALLAHAN, J. R. 1976. Systematics and biogeography of the *Eutamias obscurus* complex (Rodentia: Sciuridae). Ph.D. dissert., The University of Arizona, Tucson, 184 pp.
- . 1977. Diagnosis of *Eutamias obscurus* (Rodentia: Sciuridae). *Journal of Mammalogy*, 58:188–201.
- . 1981. Vocal solicitation and parental investment in female *Eutamias*. *The American Naturalist*, 118:872–875.
- CALLAHAN, J. R., AND D. Q. ESTEP. 1982. Tree and ground nests of southern *Eutamias*. *The Southwestern Naturalist*, 27:234–238.
- COOLEY, R. A., AND G. M. KOHLS. 1945. The genus *Ixodes* in North America. United States Public Health Service, National Institute of Health Bulletin, 184:1–246.
- DAVIS, R., AND J. R. CALLAHAN. 1992. Post-Pleistocene dispersal

- in the Mexican vole (*Microtus mexicanus*): an example of an apparent trend in the distribution of southwestern mammals. *The Great Basin Naturalist*, 52:262-268.
- DOLAN, J. M., AND M. MORAN. 1969. Historical list of *Mammalia* exhibited in the San Diego Zoological Garden. *Der Zoologische Garten*, 37:48-63.
- ELLIOT, D. G. 1904. Catalogue of mammals collected by E. Heller in southern California. Field Columbian Museum Publication 91, Zoological Series, 3:271-321.
- ELLIS, L. S., AND L. R. MAXSON. 1979. Evolution of the chipmunk genera *Eutamias* and *Tamias*. *Journal of Mammalogy*, 60:331-334.
- FERRIS, G. F. 1916. Notes on Anoplura and Mallophaga, from mammals, with descriptions of four new species and a new variety of Anoplura. *Psyche*, 23:97-120.
- . 1951. The sucking lice. *Memoirs of the Pacific Coast Entomological Society*, 1:1-320.
- FURMAN, D. P., AND E. C. LOOMIS. 1984. The ticks of California (Acari: Ixodida). *Bulletin of the California Insect Survey*, 25:1-239.
- GRINNELL, J. 1908. The biota of the San Bernardino Mountains. University of California Publications in Zoology, 5:1-170.
- . 1933. Review of the Recent mammal fauna of California. University of California Publications in Zoology, 40:71-234.
- GRINNELL, J., AND T. I. STORER. 1916. Diagnoses of seven new mammals from east-central California. University of California Publications in Zoology, 17:1-8.
- GRINNELL, J., AND H. S. SWARTH. 1913. An account of the birds and mammals of the San Jacinto area of southern California with remarks upon the behavior of geographic races on the margins of their habitats. University of California Publications in Zoology, 10:197-406.
- HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3-23, in *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.
- HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1-600 + 90.
- HILL, T. P., AND D. W. DUSZYNSKI. 1986. Coccidia (Apicomplexa: Eimeriidae) from sciurid rodents (*Eutamias*, *Sciurus*, *Tamiasciurus* spp.) from the western United States and northern Mexico with descriptions of two new species. *Journal of Protozoology*, 33:282-288.
- HOFFMEISTER, D. F. 1986. Mammals of Arizona. The University of Arizona Press and The Arizona Game and Fish Department [Tucson], 602 pp.
- HOWELL, A. H. 1929. Revision of the American chipmunks (genera *Tamias* and *Eutamias*). *North American Fauna*, 52:1-157.
- INGLES, L. G. 1965. Mammals of the Pacific states: California, Oregon, and Washington. Stanford University Press, Stanford, California, 506 pp.
- JAEGER, E. C. 1929. Denizens of the mountains. Charles C Thomas Publisher, Springfield, Illinois, 168 pp.
- . 1955. A source-book of biological names and terms. Third ed. Charles C Thomas Publisher, Springfield, Illinois, 323 pp.
- JAMESON, E. W., JR., AND H. J. PEETERS. 1988. California mammals. University of California Press, Berkeley, 403 pp.
- JOHNSON, D. H. 1943. Systematic review of the chipmunks (genus *Eutamias*) of California. University of California Publications in Zoology, 48:63-147.
- LARSON, E. A. 1981. Merriam's chipmunk on Palo Escrito in the Santa Lucia Mountains of California. Part I. Regimen with recorded episodes of naturalistic behavior. Wacoba Press, Big Pine, California, 111 pp.
- . 1986. Merriam's chipmunk on Palo Escrito in the Santa Lucia Mountains of California. Part II. The individual in relation to its environment with recorded episodes of naturalistic behavior. Wacoba Press, Big Pine, California, 283 pp.
- . 1987. Merriam's chipmunk on Palo Escrito in the Santa Lucia Mountains of California. Part III. Social relations and interactions, patterns of behavior and population changes together with recorded episodes of naturalistic behavior. Wacoba Press, Big Pine, California, 157 pp.
- LEVENSON, H. 1990. Sexual size dimorphism in chipmunks. *Journal of Mammalogy*, 71:161-170.
- LEVENSON, H., R. S. HOFFMANN, C. F. NADLER, L. DEUTSCH, AND S. D. FREEMAN. 1985. Systematics of the Holarctic chipmunks (*Tamias*). *Journal of Mammalogy*, 66:219-242.
- LINSDALE, J. M., AND B. S. DAVIS. 1956. Taxonomic appraisal and occurrence of fleas at the Hastings Reservation in central California. University of California Publications in Zoology, 54:293-369.
- NADLER, C. F., R. S. HOFFMANN, AND D. M. LAY. 1969. Chromosomes of the Asian chipmunk *Eutamias sibiricus* Laxmann (Rodentia: Sciuridae). *Experientia*, 25:868-869.
- NADLER, C. F., R. S. HOFFMANN, AND H. LEVENSON. 1985. Biochemical and morphological relationships among Holarctic chipmunks. *Acta Zoologica Fennica*, 170:19-23.
- NADLER, C. F., R. S. HOFFMANN, J. H. HONACKI, AND D. POZIN. 1977. Chromosomal evolution in chipmunks, with special emphasis on A and B karyotypes of the subgenus *Neotamias*. *The American Midland Naturalist*, 98:343-353.
- NELSON, B. C. 1980. Plague studies in California—the roles of various species of sylvatic rodents in plague ecology in California. *Proceedings of the Vertebrate Pest Conference*, 9:89-96.
- STORER, T. I., AND R. L. USINGER. 1963. Sierra Nevada natural history: an illustrated handbook. University of California Press, Berkeley, 374 pp.
- SUMNER, L., AND J. S. DIXON. 1953. Birds and mammals of the Sierra Nevada with records from Sequoia and Kings Canyon national parks. University of California Press, Berkeley, 484 pp.
- SUTTON, D. A. 1982. The female genital bone of chipmunks, genus *Eutamias*. *The Southwestern Naturalist*, 27:393-402.
- SUTTON, D. A., AND C. F. NADLER. 1969. Chromosomes of the North American chipmunk genus *Eutamias*. *Journal of Mammalogy*, 50:524-535.
- TRAUB, R., M. ROTHSCHILD, AND J. F. HADDOW. 1983. The Rothschild collection of fleas. The Ceratophyllidae: key to the genera and host relationships with notes on their evolution, zoogeography and medical importance. Academic Press, London, United Kingdom, 288 pp.
- VAUGHAN, T. A. 1954. Mammals of the San Gabriel Mountains of California. University of Kansas Publications, Museum of Natural History, 7:513-582.
- WHITE, J. A. 1953. The baculum in the chipmunks of western North America. University of Kansas Publications, Museum of Natural History, 5:611-631.
- WILSON, D. E., AND D. M. REEDER (EDS.). 1993. Mammal species of the world: a taxonomic and geographic reference. Second ed. Smithsonian Institution Press, Washington, D.C., 1206 pp.
- WUNDER, B. A. 1968. Oxygen consumption and body temperature of exercising chipmunks, *Eutamias merriami*. *American Zoologist*, 8:767.
- . 1969. Thermoregulation and the energetics of running activity in Merriam's chipmunk, *Eutamias merriami*. *Dissertation Abstracts*, 29B:3555B.
- . 1970a. Temperature regulation and the effects of water restriction on Merriam's chipmunk, *Eutamias merriami*. *Comparative Biochemistry and Physiology*, 33:385-403.
- . 1970b. Energetics of running activity in Merriam's chipmunk, *Eutamias merriami*. *Comparative Biochemistry and Physiology*, 33:821-836.
- Editors of this account were J. ALDEN LACKEY and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.
- T. L. BEST AND N. J. GRANAI, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESS HALL, AUBURN UNIVERSITY, ALABAMA 36849-5414.